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Research Article

Food web positioning of a recent coloniser: the North American Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) in the northern Baltic Sea

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Abstract

Identifying resource use and functional traits of non-indigenous species are promising means to increase the ability to predict ecological consequences of invasions. One of the most widely spread brachyuran crab species, and a recent invader in the northern Baltic Sea, is the North American Harris mud crab, *Rhithropanopeus harrisii* (Gould, 1841). Although spread, establishment, and population structure have been studied for this species, little is known about its role and impact in a new environment. We investigated the position and role of *R. harrisii* in the coastal food web by combining spatial and temporal estimates of trophic position using stable isotopes ($\delta^{13}C$ and $\delta^{15}N$), with short-term food- and habitat-choice experiments. We observed a stable pattern in the trophic position between two environmentally different locations in the Archipelago Sea over the production season. The identification of a natural breakpoint in carbon stable isotopes at the size of 12 mm carapace width suggested a presence of an ontogenetic diet shift, which was confirmed by isotope signatures positioning large *R. harrisii* among secondary consumers and small individuals with primary consumers. The generalist consumer nature of *R. harrisii* and preference for structured habitat was supported by an active habitat and food choice, revealing no preference for prey species (polychaetes versus amphipod), but selection of brown algae over bare mud. To broaden the understanding of the functional role of *R. harrisii*, we combined our findings with other known biological and ecological traits of the species and qualitatively compared these to characteristics of other benthic organisms in the northern Baltic Sea, suggesting a general similarity in traits.

Key words: introduced species, feeding, habitat choice, stable isotopes, biological traits, experiment

Introduction

Human-mediated species introductions are a continuing threat to both terrestrial and marine biodiversity and thus an important part of global change (Strayer 2012; Simberloff et al. 2013; Jeschke et al. 2014). To increase our ability to predict ecological changes due to non-native species introductions, invasion ecology needs to move beyond descriptive cataloguing of establishment and impact studies and to a more mechanistic understanding and quantification of invader effects (Dick et al. 2014; Paterson et al. 2015). The most promising efforts to generalise mechanisms have focused on how non-indigenous species alter communities and ecosystems through resource use (Vitousek 1990; Parker et al. 1999; Dick et al. 2014). Differences in resource use, such as food or habitat, are reflected in practically all of the 29 hypotheses designed to explain invasion success summarised by Catford et al. (2009). For many of these hypothesis, a major factor that influence invasion success is related to the biological characteristics of the invading species and/or species in the recipient community (Catford et al. 2009; Dick et al. 2014). Recent progress in comparisons of species traits between invaders and natives is encouraging in assessing establishment and spread of invaders (Dick et al. 2014), particularly for terrestrial plant species (Van Kleunen et al. 2010) and to some degree for fish (Marchetti et al. 2004), but still remains patchy (Hayes and Barry 2008; Dick et al. 2014). Moreover, characterising and quantifying traits of non-native species to specifically assess impact is also emerging (Dobb et al. 2014; Paterson et al. 2015). In one study, a comparison between marine invasive invertebrates in only one trait, size,

revealed effects on the invading species itself (Grosholz and Ruiz 2003). Gribben et al. (2013) examined several traits in a biogeographic evaluation of the porcelain crab *Petrolisthes elongatus* (H. Milne-Edwards, 1837) while Gothland et al. (2014) described biological traits related to colonisation and distribution Asian shore crab *Hemigrapsus takanoi* Asakura and Watanabe, 2005. The current gap in the use of species' ecological knowledge between invasion ecology and other ecological fields is interesting because trait-based approaches have proven successful for disentangling marine biodiversity-ecosystem functional linkages (Solan et al. 2006), macroecological patterns (Webb et al. 2009), and anthropogenic impacts (Bremner et al. 2006; de Juan et al. 2007; Villéger et al. 2010).

Some mesohaline habitats, particularly in higher latitude areas, are characterized by relatively low species numbers and relatively weak interspecific competition interactions, which provides the opportunity for colonization by non-indigenous species (Cohen and Carlton 1998; Stachowicz et al. 2002). The Baltic Sea has abiotic and biotic conditions seemingly ideal for establishment of introduced species (Paavola et al. 2005; Gollash and Leppäkoski 2007; Leppäkoski et al. 2009). This mainly brackish (salinity 0.5–20) water body is geologically young (< 10,000 years), with a biota consisting of post-glacial immigrants (Bonsdorff 2006; Leppäranta and Myrberg 2009). Native species diversity is low, which results in simple food webs with relatively few links (Bonsdorff and Blomqvist 1993; Elmgren and Hill 1997). To date, 119 non-indigenous species have been found in the Baltic Sea, of which 20 species have been reported in the northern Baltic Sea and the Archipelago Sea area (David et al. 2013), which is the region of focus in this study. One of the more recent invaders in the northern Baltic Sea is the North American Harris mud crab, *Rhithropanopeus harrisii* (Gould, 1841). The species is a small (adult maximum carapace width 25 mm) brachyuran crab that tolerates a wide range of temperatures (4–35°C) and salinities (0.5 to >40) (Costlow et al. 1966; Forward 2009). The native range of *R. harrisii* extends along the Atlantic coast of North America from the Gulf of St Lawrence in Canada to Veracruz in the Gulf of Mexico, where it occupies a wide variety of substrates and habitats in river mouths and estuaries (Williams 1984; Fowler et al. 2013). The species was already known in Europe in 1874, probably arriving in ballast water. *R. harrisii* was first found in the southern Baltic Sea in the 1950s, where it has since become established (Turoboyski 1973; Hegele-Drywa and Normant 2014). In the Archipelago Sea, *R. harrisii* was first recorded in 2009, and it has since established reproducing populations in more than 80 locations within a 30 km radius of the site of initial colonization (Fowler et al. 2013). Apart from the occasional adult Chinese mitten crab (*Eriocheir sinensis* H. Milne-Edwards, 1853) (Anger 1991), there were no other crab species in the northern Baltic Sea prior to the arrival of *R. harrisii* (Ojaveer et al. 2007).

The establishment and spread of *Rhithropanopeus harrisii* globally and in the Baltic Sea is well catalogued, but few studies have assessed the impact of this species on the recipient community and ecosystem. Similar to other non-indigenous crab species (e.g., Goodenough 2010; Brockernhoff and McLay 2011), there is clear evidence of competition between *R. harrisii* and native crabs and benthivorous fishes at sites in Europe and on the west coast of North America (Cohen and Carlton 1995; Zaitsev and Öztürk 2001). The species also alters the local food webs because *R. harrisii* is both a predator on, and prey for, native species (Turoboyski 1973; Cohen and Carlton 1995; Zaitsev and Öztürk 2001; Fowler et al. 2013). *R. harrisii* is an opportunistic omnivore that feeds on a mixture of animals, vegetation, and detritus (Turoboyski 1973; Czerniejewski and Rybczyk 2008; Hegele-Drywa and Normant 2009). As in its native range, the species occupies a diverse array of substrates in the northern Baltic Sea, including: bare soft sediment, stones, decaying reeds (*Phragmites australis* (Cav.) Trin. ex Steud.), brown algae (*Fucus vesiculosus* Linnaeus, 1753) and other vegetation that provide both protection and a high density and rich variety of prey (Fowler et al. 2013; Nurkse et al. 2015).

The overall aim of this study was to investigate the trophic position and role of *Rhithropanopeus harrisii* in the coastal food web of the northern Baltic Sea. We addressed this by combining spatial and temporal estimates of trophic position of *R. harrisii* with short-term habitat- and food choice experiments. More specifically, we wanted to: i) determine ontogenetic differences in trophic position of *R. harrisii*; ii) assess temporal variability of the species' consumer characteristics; and iii) identify whether *R. harrisii* displays an active choice for selected substrates and prey species. We then qualitatively compared the known biological and ecological traits of *R. harrisii* to other benthic organisms in the northern Baltic Sea as a means of evaluating the

effects of introduction of *R. harrisii* on ecosystem structure and functioning.

Acknowledging that the diet of generalist predators rely on the spatial and temporal availability of food items (Evans 1983), we assessed trophic position of Harris mud crab by investigating variability in stable isotopes ratios (^{13}C:^{12}C and ^{15}N:^{14}N, expressed as $\delta^{13}C$ and $\delta^{15}N$) (Peterson and Fry 1987). Earlier studies (e.g. Nordström et al. 2009, 2010; Karlson et al. 2015) demonstrated spatial and temporal differences in food web structure between various shallow coastal habitats in the northern Baltic Sea. Therefore, we focused our work on two habitats that differed with respect to wave exposure and substrate. To accommodate potential temporal differences during the productive season, we conducted field sampling in both early and late summer. We hypothesized that the two populations of *R. harrisii* would experience somewhat different food availability, which could reveal the plasticity of the species in their food web positioning. In accordance with present knowledge about the species' use of resources, we hypothesised that *R. harrisii* individuals would actively choose prey and favour a structurally more complex and potentially more sheltering habitat over bare substrate.

Methods

Trophic positioning through stable isotope analysis

To assess trophic position, we collected *Rhithropanopeus harrisii* individuals, fish, benthic infauna and epifauna, vascular plants, algae, and detritus from two localities in the Archipelago Sea in June and August 2012. Sampling sites were located 30 km apart in the inner archipelago zone, with a salinity of 5–6 and depth of 1–2 m. The two sites differed markedly in terms of wind and wave exposure as well as the composition of the bottom substrate. Sampling station 1 (Tuorla: 60°40′77″N; 22°44′29″E) was situated in a narrow and shallow strait in the inner archipelago, where vegetation along the shores were dominated by the European common reed *Phragmites australis*. The bottom consisted of mud, which was covered by decaying reeds, and the sediment was sometimes hypoxic under the overlying vegetation. Sampling station 2 (Lempisaari: 60°49′04″N; 21°77′90″E) was situated further out in the archipelago, still surrounded by islands but leaving it more exposed to wind and wave action. Perennial brown algae (*Fucus vesiculosus*) and common reed dominated the vegetation in the area. The bottom consisted of mud and clay, covered by a layer of loose drifting *F. vesiculosus*.

Sampling of *R. harrisii* was accomplished using wire traps filled with shells or pieces of clay pots that allowed crabs to move in and out freely (Fowler et al. 2013). Some of the crabs at station 2 were collected by hand from drifting stands of *F. vesiculosus*. Fish were collected from some of the crab traps, and additional fish samples were collected with a wire fish-trap (20 mm mesh size). Epi- and in-faunal benthic invertebrates were sampled using an Ekman-Birge grab and push-nets. Plant material and algae were sampled with push-nets and rakes. Thirty two taxa (plants, invertebrates, and fish) were sampled in this study: 26 taxa from station 1 and 24 taxa at station 2, with 18 taxa in common (Table 1).

All samples were frozen as soon as possible and stored at -20 °C for subsequent analyses. In the laboratory, crabs were measured (carapace width, CW in mm), and the sex was determined if possible. The smallest crab for which we could determine to sex was 7 mm CW. However, sex was not determined for many crabs collected in June (station 1: 40 individuals; station 2: 50 individuals). These crabs were mostly 4–10 mm CW.

Depending on the size of the crab, claw muscle tissue, whole claws, or the whole individual was used for analysis of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) stable isotopes. Muscle tissue was used from fish and the Baltic prawn *Palaemon adspersus* Rathke, 1837. Specimens of epi- and in-faunal benthic invertebrates were analysed whole, except bivalves and gastropods for which shell-free soft tissues were used. Three to five individuals were sampled from each species. All samples were treated with 1 M HCl to remove carbonates. The animal material was dried at 60 °C for 48 h, crushed to a powder in a mortar, and 1 (± 0.2) mg of the sample put into tin capsules for analysis. Plant material was dried, crushed to a powder, and 2–3 mg of the powder was put into tin capsules for analysis. The samples were sent to the Stable Isotope Facility of the University of California, Davis (California, USA) for analysis of carbon and nitrogen stable isotope ratios.

Habitat- and food choice experiments

The individuals of *R. harrisii* used in the laboratory experiments were collected two weeks prior to the experiments and were kept in 30 L aquaria filled with seawater (15 °C, salinity 5.5) and equipped with an aerating system. Pieces of

Table 1. List of sampled foodweb components found on Station 1 and Station 2 in 2012. A species/food web component found in only one station is indicated in bold.

Secondary consumers:	Station 1	Station 2
Rhithropanopeus harrisii	x	x
Palaemon adspersus	x	x
Perca fluviatilis	x	x
Gymnocephalus cernuus	**x**	
Gobius niger	x	
Pomatoschistus minutus	x	x
Pungitus pungitus	**x**	x
Rutilus rutilus	x	
Tinca tinca	x	x
Abramis brama	**x**	x
Blicca bjoerkna	**x**	
Scardinius erythrophthalmus	**x**	
Primary consumers:		
Asellus aquaticus	x	x
Gammarus sp.	x	x
***Marenzelleria* sp.**		**x**
Hediste diversicolor		**x**
Macoma balthica	x	x
Mya arenaria		**x**
Mytilus edulis		**x**
Theodoxus fluviatilis	x	x
Lymnea stagnalis	x	x
Bithynia tentaculata	x	x
Chironomidae	x	x
Ephemeroptera	x	x
Odonata	x	x
Tricoptera	**x**	
Primary producers:		
Ceratophyllym demersum	x	x
***Myriophyllum* sp.**	**x**	
Cladophora glomerata	x	x
Enteromorpha intestinalis	**x**	
***Fucus vesiculosus* (apikal and**		**x**
basal)		**x**
Epiphytes (on *F. vesiculosus*)		
Detritus	x	x
Decaying *Phragmites australis*	**x**	

clay-pots were added to the aquaria to provide shelter for the crabs, and the individuals were fed frozen chironomids and clams (*Macoma balthica* (Linnaeus, 1758)) during this time. Individuals were fasted for 24 hours prior to the experiments. Both male and female crabs (mean ± SE CW: 16.1 ± 0.32 mm; range: 8.4 to 21.4 mm; n = 60) were used in the experiments but no distinction was made between the two sexes in experiments.

The habitat- and food-choice experiments were conducted in Y-shaped aquaria, which allows for a combination of two resources to be presented to the individual crab simultaneously (Bonsdorff and Vahl 1982). We used two experimental aquaria (basal area: 40 × 16 cm; each arm area: 33 × 10 cm; water height: 8 cm; water volume: 6 L) to conduct trials. A trial consisted of a combination of either two resources or a resource and a control (three possible combinations), and was repeated 15 times. Experimental trials were randomised between the two aquaria, and new individuals were used every trial to avoid any bias in individual crab behaviour or related to the experimental conditions. The aquaria was scrubbed and carefully rinsed with fresh water between trials to remove all traces of the resources. The placement of a resource (habitat or food) or control (seawater, no substrate) in the end of either of the two "arms" was randomised for each trial. The water temperature was kept at 15 °C, salinity at 5.5, and a flow-through system allowed water to flow from each "arm" to the basal area at a rate of 0.15 L/minute, resulting in 100 % water exchange every 40 minutes.

Prior to the start of the experiment, a crab was placed at the basal area, where it was allowed to acclimatize for 10 minutes. A perforated wall between the base and the "arms" prevented the crab from leaving the basal area, but exposed the individual to the water from the "arms" and thereby the potential odour from the resources. When an experimental trial started, the perforated wall was lifted, and we noted the initial choice of the crab and then documented the position of the crab every five minutes for 30 minutes, providing six observations per trial.

In the habitat choice experiment, crabs could choose between soft sediment (clay) and brown algae (*Fucus vesiculosus*). In the food choice experiment, we used the vegetation-associated amphipod *Gammarus* spp. and the sediment-dwelling polychaete *Hediste diversicolor* O. F. Müller, 1776 as food resources. Both prey species were placed inside a transparent net-bag that allowed the crabs to see and smell the prey without consuming it. The control in both the food- and habitat experiment was seawater, no substrate.

Statistical analyses

As a first step, to evaluate if there were any natural breakpoints in carbon isotope values in relation to size of the crab, we conducted a piecewise linear regression analysis using the package Segmented (Muggeo 2008) in R (R Development Core Team 2014). The results showed that there were two breakpoints, one at 11.53 ± 0.36 mm CW and another at 12.32 ± 0.11 mm CW (mean ± SE)

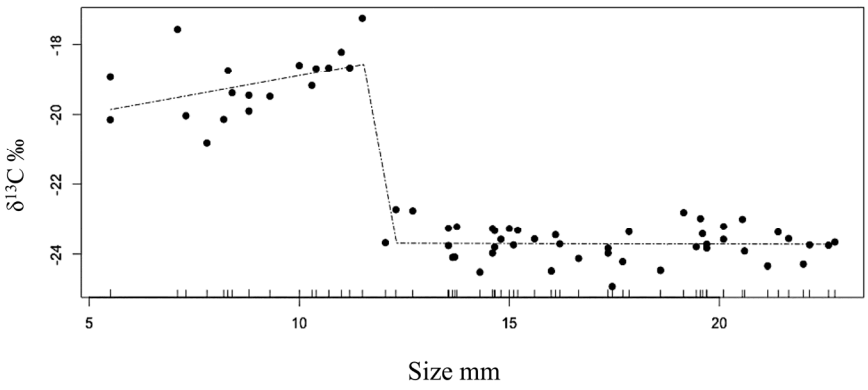

Figure 1. Piecewise regression plot of *Rhithropanopeus harrisii* size (x-axis) versus $\delta^{13}C$ –values (y-axis) of all crabs sampled in June and August 2012. Two breakpoints are identified at around 12 mm carapace width size. Slopes of the lines are 0.2163 (for size up to 11.53 mm), -6.529 (11.53 – 12.32 mm) and -0.00271 (> 12.32 mm).

Table 2. Number, sex, and size (carapace width range and mean size, mm) of *Rhithropanopeus harrisii* sampled at Station 1 and Station 2 in June and August 2012.

	June			August		
	n	range	mean ± SE	n	range	mean ± SE
a) Station 1						
Male	17	14.3 – 22.0	18.45 ± 0.60	26	7.45 – 22.75	15.04 ± 0.96
Female	10	13.5 – 16.2	14.97 ± 0.30	15	7 – 13.55	10.32 ± 0.49
Not sexed	40	4.0 – 12.0	7.52 ± 0.28	0		
Total	67			41		
b) Station 2						
Male	6	11.7 – 19.3	16.60 ± 1.16	16	10 – 20.5	15.78 ± 0.87
Female	13	10.0 – 17.5	12.45 ± 0.77	0		
Not sexed	50	4.0 – 10.0	6.70 ± 0.24	8	10 – 15	11.49 ± 0.76
Total	69			24		

(Figure 1). Thus, for all subsequent analysis, we divided crabs into small (< 12 mm CW) and large (> 12 mm CW) size classes.

To assess spatial differences in stable isotope values of small and large size classes of *R. harrisii* and food web components (detritus, primary producers, primary and secondary consumers), separate t-tests were used. If the variances were not homogenous, a *t*-test with Welch correction was performed.

In order to assess temporal differences in isotope values between the two size classes, we conducted separate Two-way ANOVAs for station 1 and station 2 for both $\delta^{13}C$ and $\delta^{15}N$. A comparison of isotopic differences between male and female crabs was analysed with *t*-tests for the large sized crabs (> 12mm CW) in June only, as not enough data were available for comparison in August.

To analyse the first-choice (resources or control) of crabs in the aquarium experiments, we used Chi-square statistics. One-way ANOVA was used to analyse the choice of crabs made every 5 minutes (i.e. the position of the crabs in the aquaria), during the 30 min trial. No data transformations were required as the data were normally distributed and the variances homogeneous.

Results

Trophic position and spatial variability

We collected 108 (48 large, 60 small) individuals of *R. harrisii* at station 1 and 93 (26 large and 67 small) at station 2 (Table 2). The largest number of individuals was sampled in June at both stations, and the majority were smaller than 12 mm CW (60 % at station 1 and 84 % at station 2). In August, the small size group accounted for 50 % of the individuals from station 1 and 38 % of those from station 2. The sex ratio was skewed toward more males at both sampling sites. However, in June, sex was not determined for most crabs due the small individual sizes of the animals. Five ovigerous females (38% of all female crabs, 10.7–13.6 mm CW) were obtained from

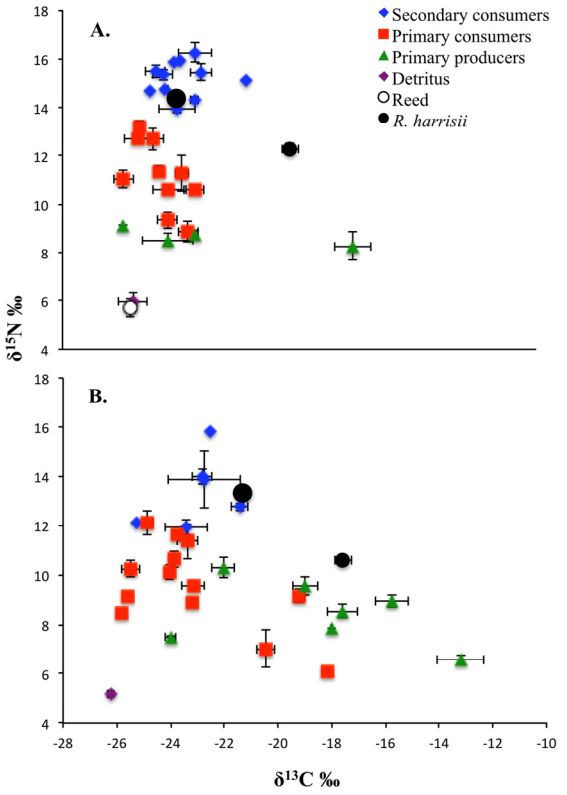

Figure 2. Isotope values ($\delta^{13}C$ & $\delta^{15}N$) for organisms sampled in June and August 2012, at A. Station 1 (Tuorla) and B. Station 2 (Lempisaari). Large (> 12 mm) and small (< 12 mm) *Rhithropanopeus harrisii* are indicated by larger and smaller symbol (•), respectively. Secondary consumers: *Abramis brama*[1], *Blicca bjoerkna*[1], *Gobius niger*, *Gymnocephalus cernuus*[1], *Palaemon adspersus*, *Perca fluviatilis*, *Pomatoschistus minutus*, *Pungitus pungitus*[1], *Rutilus rutilus*, *Scardinius erythrophthalmus*[1], *Tinca tinca*. Primary consumers: *Asellus aquaticus*, *Bithynia tentaculata*, Chironomidae, Ephemeroptera, *Gammarus* sp, *Lymnea stagnalis*, *Macoma balthica*, *Marenzelleria* sp[2], *Mya arenaria*[2], *Mytilus edulis*[2], *Hediste diversicolor*[2], Odonata, *Theodoxus fluviatilis*, Tricoptera[1]. Primary producers: *Ceratophyllym demersum*, *Cladophora glomerata*, *Enteromorpha intestinalis*[1], Epiphytes (on Fucus)[2], *Fucus vesiculosus* (apical)[2], *F. vesiculosus* (basal)[2], *Myriophyllum* sp. [1]= species were found on station 1 only, [2] = species were found on station 2 only.

station 1 in August, while only males were found at station 2 at that time.

The stable isotope values (June and August combined) of *R. harrisii* at station 1 varied between -24.90 and -17.58 ‰ for $\delta^{13}C$ and between 10.59 and 15.47 ‰ for $\delta^{15}N$ (Figure 2A). Crab individuals at station 2 were enriched in carbon compared to the other station (-22.69 and -15.19 ‰ for $\delta^{13}C$) and depleted in nitrogen (between 9.07 and 14.31 ‰ for $\delta^{15}N$) (Figure 2B). This pattern was confirmed for both the large and small size class of crabs when we compared mean values of $\delta^{13}C$ of *R. harrisii* between stations (large: $t = 13.60$, df = 31, $p < 0.0001$, and small: $t = 3.646$, df = 35, $p = 0.0009$). Similarly, both size classes differed significantly in terms of $\delta^{15}N$ between stations (large: $t = 5.733$, df = 63, $p < 0.0001$, and small: $t = 4.383$, df = 38, $p < 0.0001$).

The same spatial variability in carbon and nitrogen signatures was also found within the other food web components except detritus, which did not vary between stations (Figure 2). At station 1, the values for all sampled food web components ranged between -15.4 and -27.7 for $\delta^{13}C$ and between 3.4 and 17.3 for $\delta^{15}N$. At station 2, the corresponding values were -10.7 to -26.5 for $\delta^{13}C$ and 3.6 to 15.8 for $\delta^{15}N$. Both secondary and primary consumers were significantly enriched in $\delta^{13}C$ at station 2 compared to station 1 (secondary consumers: $t = 3.251$, df = 51, $p = 0.0020$, primary consumers: $t = 6.099$, df = 64, $p < 0.0001$). Carbon stable isotope values of primary producers did not differ significantly between sites. Similarly, a significantly higher $\delta^{15}N$ value was found at station 1 for secondary ($t = 7.207$, df = 51, $p < 0.0001$) and primary consumers ($t = 5.800$, df = 65, $p < 0.0001$), as well as primary producers ($t = 3.994$, df = 9, $p = 0.0031$).

In terms of the spatial variability in trophic position of the two size classes, the same pattern was seen at both stations. The large size class of *R. harrisii* was located at the same trophic level as fish and other secondary consumers, while small individuals were positioned together with primary consumers, in this case invertebrates (Figure 2). This result supports the clear evidence of an ontogenetic diet change, as initially suggested in the piece-wise linear regression (Figure 1).

Temporal variability of isotope signatures

Carbon and nitrogen stable isotopes of the two size-classes varied over time but the general difference between large and small crabs were constant at both stations. At station 1, a significant interaction between crab size and month was detected for both $\delta^{13}C$ and $\delta^{15}N$ values (Table 3). The average $\delta^{13}C$ value at station 1 in June was 4 ‰ higher in large crabs than small ones (Figure 3), i.e., large crabs were more enriched in carbon. In August, the difference was almost 5 ‰ between

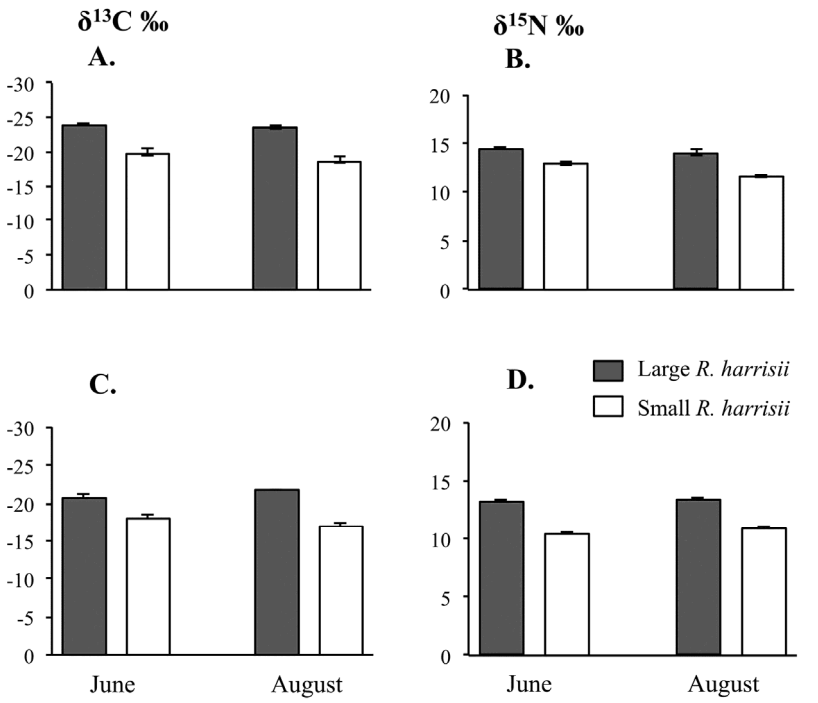

Figure 3. $\delta^{13}C$ and $\delta^{15}N$ for large (> 12 mm carapace width) and small (< 12 mm carapace width) *Rhithropanopeus harrisii* collected in June and August 2012. A. and B. Station 1, C. and D. Station 2. Values are mean ± SE. See Table 3 and Table 4 for significant differences.

Table 3. Two-factor ANOVA results of a) $\delta^{13}C$ and b) $\delta^{15}N$ in *Rhithropanopeus harrisii* of different sizes (small, large) and sampled in different months (June, August) at Station 1. Significant differences are shown in bold.

Treatment	df	MS	F	p
a) $\delta^{13}C$				
Size	1	248.5	831.0	**<0.0001**
Month	1	6.279	21.00	**<0.0001**
Size × Month	1	2.600	8.694	**0.0046**
Error	57	0.2990		
b) $\delta^{15}N$				
Size	1	52.58	119.6	**<0.0001**
Month	1	10.36	23.56	**<0.0001**
Size × Month	1	3.041	6.918	**0.0110**
Error	57	0.4396		

Table 4. Two-factor ANOVA results of a) $\delta^{13}C$ and b) $\delta^{15}N$ in *Rhithropanopeus harrisii* of different sizes (small, large) and sampled in different months (June, August) at Station 2. Significant differences are shown in bold.

Treatment	df	MS	F	p
a) $\delta^{13}C$				
Size	1	159.5	135.0	**<0.0001**
Month	1	0.9287	0.7862	0.3806
Size × Month	1	8.387	7.100	**0.0111**
Error	40	1.181		
b) $\delta^{15}N$				
Size	1	64.80	88.79	**<0.0001**
Month	1	0.1559	0.2136	0.6464
Size × Month	1	0.02149	0.02945	0.8646
Error	40	0.7298		

the size categories at the same station. The mean $\delta^{15}N$ was 1.57 ‰ higher in large sized crabs compared to small ones in June and 2.57 ‰ higher in August (Figure 3). The $\delta^{13}C$ values of large (> 12 mm) crabs did not differ significantly ($p = 0.7630$) between males and females in June, whereas $\delta^{15}N$ values were significantly higher in females than in males ($t = 2.563$, $df = 25$, $p = 0.0154$).

A slightly different pattern was observed at station 2, where a significant interaction between crab size and month was detected for $\delta^{13}C$ but not for $\delta^{15}N$ (Table 4). In parallel to station 1, large crabs were more enriched in carbon compared to small ones and this increased over time (average value of $\delta^{13}C$ in June was 3 ‰ higher for the larger size class and increased to 4.8 ‰ in August) (Figure 3). Concerning $\delta^{15}N$, values differed significantly between the two size classes but not over time (between June and August). The $\delta^{15}N$ values were about 2.5 ‰ higher in large sized crabs compared to the small ones in both months (Figure 3). The isotope values of large crabs did not differ significantly between the sexes ($\delta^{13}C$ $p = 0.1017$; $\delta^{15}N$ $p = 0.1312$).

Habitat and food choices

The laboratory experiments showed that *Rhithropanopeus harrisii* actively choose both habitat and prey. There was no significant difference in the initial choice of substrate, whether the crabs were presented with *Fucus vesiculosus* and control ($p = 0.80$), clay and control ($p = 0.80$), or between the two substrates ($p = 0.45$). Over the 30-minute period, however, individuals preferred *F. vesiculosus* to both control and clay (One-way ANOVAs: $F_{1,28} = 32.02$, $p < 0.0001$ and $F_{1,28} = 3.85$, $p = 0.01$, respectively). No significant difference ($p > 0.05$) was found between clay and control.

The initial food choice of *R. harrisii* varied depending on the prey species presented. Crab individuals chose the worm *H, diversicolor* over the control with seawater ($\chi^2 = 9.320$, $df = 1$, $p = 0.0023$), but showed no significant preference between *Gammarus* sp. and control ($p = 0.44$), or between *H. diversicolor* and *Gammarus* sp ($p = 0.80$). When observing the crabs for 30 minutes, however, the individuals spent significantly more time in the area of the aquaria with a food source than in the area with a control (*Gammarus* sp.: One-way ANOVA. $F_{1,28} = 4.31$, $p = 0.05$; *H. diversicolor*: $F_{1,28} = 11.48$, $p = 0.0001$). Similarly to the results of the initial choices, no clear preference of *R. harrisii* between *H. diversicolor* and *Gammarus* sp. was observed over time.

Discussion

We determined the trophic position of Harris mud crab using stable isotope ratios, and identified consistent size-specific differences over time and space. The presence of an ontogenetic diet shift was confirmed through the combination of: i) a natural breakpoint in carbon stable isotopes identified at the size of 12 mm CW; and ii) the positioning of large *Rhithropanopeus harrisii* among the secondary consumers and small individuals with primary consumers. The generalist nature of *R. harrisii* described by the stable isotope ratios was supported by an active food choice but no specific preference for the prey species presented in laboratory experiments. Our hypothesis about substrate preferences of *R. harrisii* was confirmed experimentally by the choice of the structurally more complex bladderack, *Fucus vesiculosus*, over bare mud.

The trophic role(s) resulting from ontogenetic diet shift

Depending on the diet, species may contribute to different trophic pathways and thus, express different trophic roles in an ecosystem (Blondel 2003). Moreover, ontogenetic diet shifts can result in differing juvenile and adult resource use and thus their ecological roles (Werner and Gilliam 1984). Ontogenetic changes in diet are a very common occurrence among invertebrates and fishes (Werner and Gilliam 1984) and are a means to decrease intraspecific competition for food (Aarnio et al. 1998; Arim et al. 2010; Toscano and Griffen 2012). The natural breakpoint in carbon stable isotopes of Harris mud crab at 12 mm CW suggested that large and small *R. harrisii* used different carbon sources and thus there was an ontogenetic diet shift. The analysis of *R. harrisii* stable isotope ratios in bivariate δ -space further supported this observation with small individuals acting as primary consumers while large crabs grouped with fish and other secondary consumers. The enriched $\delta^{13}C$ values of the individuals in the small size class showed that these had predominately fed on plant material, such as detritus, algae and/or macrophytes. Large crabs appeared to have fed mainly upon invertebrate fauna, which had a carbon signature about 2 ‰ lower than the signature of the crabs themselves.

Previous studies have classified the Harris mud crab as an omnivore feeding on detritus and a large variety of macrofaunal species (Turoboyski 1973). Studies based on stomach contents have had the same conclusion (Czerniejewski and Rybczyk

2008; Hegele-Drywa and Normant 2009). However, previous studies either did not take size into account (Czerniejewski and Rybczyk 2008) or focussed on crabs > 12 mm CW (Hegele-Drywa and Normant 2009). While the species *per se* can be classed as an omnivore (Pimm and Lawton 1978), our findings indicate this to be an over-simplification. The demonstrated ontogenetic switch between feeding as a primary consumer to feeding as a secondary consumer illustrates two distinct trophic roles of *R. harrisii*. In addition, ovigerous females as small as 8.4 mm CW can be found (Fowler et al. 2013; this study), which would mean that the smaller size class (<12 mm CW) includes reproductive individuals and thus is not strictly comprised of juveniles. This makes the ontogenetic diet change and the role as primary consumer interesting because it cannot be explained solely as behaviour linked to the juvenile stage.

The clear difference in trophic position with size is perhaps not surprising in the light of general invertebrate and crab ecology (Werner and Gilliam 1984; Boudreau and Worm 2012). For the invasive crab *Hemigrapsus sanguineus* (De Haan, 1835), Griffen et al. (2012) showed that herbivory decreased with increasing size for females. The shift to more animal tissue in the diet with an increase in crab age/size was assumed to reflect changes in size-specific nutritional requirements (related to molting and growth), and reflected the greater capability of larger individuals to find and handle animal prey (Griffen et al. 2012). These are also possible mechanisms for the observed shift in *R. harrisii* in this study, as are the potential need for an animal-based food source to facilitate energy need for reproduction (Kang and Poulet 2000). Nevertheless, with the existence of mature individuals < 12 mm CW, reproduction clearly occurs on a diet of detritus and other plant material. The lower consumption of animal prey by small crabs could potentially also be linked to differences in habitat usage, and thus food availability, by small and large crabs because of intra-specific competition or predation (Dittel et al. 1995; Nurkse et al. 2015).

When interpreting stable isotope signatures, nature of the tissue analysed needs to be taken into account especially for nitrogen stable isotope analysis. The lower $\delta^{15}N$ values in the small size class could be partly due to small crabs being analysed as whole organisms while only soft claw tissues were analysed for large crabs. This methodological discrepancy was inevitable because of the small amount of soft tissue material in small crabs. Søreide and Nygård (2012) showed in their study that $\delta^{15}N$ values in arctic amphipods were significantly lower in the exoskeleton than in soft tissue, and whole organism signatures were in between the two. Also, $\delta^{15}N$ values of the whole animals were 1–2 ‰ lower than those of soft tissue, while $\delta^{13}C$ values were not significantly different between whole-animal and exoskeleton samples.

Spatial and temporal consistency in trophic position

Variability in isotopic signatures in space and time is common. In this study, the trophic structure of the assemblages sampled and the position of both size-classes of *Rhithropanopeus harrisii* were consistent in space (i.e. between two different locations, about 30 km a part). Although $\delta^{15}N$ and $\delta^{13}C$ values differed significantly between the two stations studied, both regarding the whole consumer assemblage and *R. harrisii* in particular, we perceived these as resulting from local nitrogen and carbon dynamics, rather than changes in trophic level. A similar pattern in spatial variability was identified by Nordström et al. (2010) in a study of nine shallow sandy sediment food webs in the northern Baltic Sea where the basic food web components remained the same but the trophic positioning of each varied depending on the local conditions and the local species composition. Furthermore, slight differences in trophic structure and/or positioning of individual species do not necessarily indicate altered or different functional properties of the systems (Törnroos et al. 2013). Moreover, influx of freshwater can affect the natural abundances of $\delta^{15}N$ in plant tissue as allochthonous nitrogen differs in isotopic signature from autochthonous nitrogen (Peterson and Fry 1987; McClelland and Valiela 1998), while enrichment of $\delta^{15}N$ in primary producers is known to indicate denitrification, e.g., during hypoxia (Fourqurean et al. 1997). These mechanisms may explain the higher $\delta^{15}N$ values at station 1, which is a sheltered narrow strait in the inner archipelago close to the coast with a higher volume of fresh water runoff. Additionally, we noted that the sediment at station 1 occasionally experienced hypoxic conditions during the field sampling.

To be able to extrapolate results from stable isotope analysis, it is also important to assess temporal variability in isotope signatures (Akin and Winemiller 2006; Nordström et al. 2009). In this study, we were interested in the intra-seasonal variation in the trophic role of Harris mud crab, and the consistent temporal variability in signatures of large and small *R. harrisii* over the production

period (June to August) strengthened the size-specific difference in trophic position. Temporal fluctuations in stable isotope signatures is common as primary producers often vary in isotope values several times per year (Rolff 2000), which will after a potential lag time be reflected in higher trophic levels (Goering et al. 1990; Nordström et al. 2009). Our results show that the pattern was stable over time although the difference in $\delta^{13}C$ between small and large crabs increased from June to August at both locations, possibly due to changing isotope values at the base of the food web or changes in food sources, or both (Nordström et al. 2009).

The implication of an active habitat and food choice

Investigating both habitat and feeding choices is important for disentangling invasion impacts and success (Marchetti et al. 2004). As discussed above, trophic patterns may reflect differences in habitat occupancy linked to local food availability and community interactions (Dittel 1995; Nurkse et al. 2015). The results from the laboratory experiments showed that *R. harrisii* preferred the brown alga *Fucus vesiculosus* as habitat over clay or the control (no substrate), and that the crabs were strongly attracted to the odour of both prey organisms offered as food. Crabs in general have well-developed olfactory senses (Weissburg and Zimmer-Faust 1993), and *R. harrisii* uses this trait in search for both suitable habitat and food (Kidawa et al. 2004). Surprisingly, there was no difference between the choice of clay and bare substrate as alternative habitats, although clay naturally had a stronger odour than plain seawater. The burying behaviour of Harris mud crab is well known (Petersen 2006; Fowler et al. 2013) and females in particular need access to suitable sediments when they are about to lay their eggs (Turoboyski 1973). During other periods, crabs are observed to search for shelter under shells, stones, or in vegetation (Ryan 1956; Fowler et al. 2013). We used both male and female individuals in our experiments, and both were primarily attracted to the habitat that provided overhead shelter over clay and the structure-free control. These findings are consistent with other experiments (Nurkse et al. 2015) in which *R. harrisii* chose habitats with boulders covered with *F. vesiculosus* over all other habitats provided (*Cladophora*, unvegetated boulder, silty sand).

In the food choice experiment, both prey species were chosen over the control, but no preference was found between the offered prey types. Our experimental results support previous findings that the species chooses prey according to availability (Czerniejewski and Rybczyk 2008; Hegele-Drywa and Normant 2009). The preferred first choice was the polychaete *Hediste diversicolor*, however, no statistical differences in overall choice were found. It is possible that *H. diversicolor* left a stronger chemical cue in the water than the amphipods (Velez et al. 2007) and was thus detected more easily by the crabs. In line with studies of olfactory senses in other crab species (Rittschof 1992; Keller et al. 2003) and crustaceans (Weissburg and Zimmer-Faust 1993; Lee and Meyers 2006), the strength of a food signal may be a significant factor modifying food-search behaviour of *R. harrisii*. Kidawa et al. (2004) demonstrated that *R. harrisii* uses the stimulus concentration as a source of information about their distance to a food item. Furthermore, avoidance behaviour of weak food signals may decrease the risk of encountering predators or cannibalistic conspecifics (Kidawa et al. 2004; Tran 2014). Additionally, crabs exposed to food odour repeatedly may lose their motivation to locate the food if they cannot find its source and begin feeding (Ristvey and Rebach 1999; Kidawa et al. 2004). The crabs in our experiments may have lost interest in the prey because they could not reach it through the net-bags, which could explain why there was no difference between choices of prey species over the 30 min period.

Understanding of the trophic and functional roles of non-indigenous species

Recent studies on the role of non-indigenous species in the marine environment underlines the importance of knowing their biology and ecology as a basis for legislation and marine management (Lehtiniemi et al. 2015; Ojaveer et al. 2015), as well as impact prediction (Kolar and Lodge 2001; Dick et al. 2014). We therefore gathered the current biological and ecological trait knowledge of this species worldwide (Table 5) and qualitatively compared a number of traits with those of the native macrofaunal community (from Valanko et al. 2010; Villnäs et al. 2011; Törnroos and Bonsdorff 2012; Törnroos et al. 2015). Törnroos and Bonsdorff (2012) described 12 trait categories expressed by the macrofaunal community along the entire Finnish coastline, i.e., represented the typical functional characteristics of the northern Baltic Sea benthic species. *Rhithropanopeus harrisii* shares eight of these traits with this "type organism" because *R. harrisii* is: of medium size (1–3 cm); reproduces sexually and has separate sexes; is mobile; and

Table 5. Compilation of traits and ecologically important information of *Rhithropanopeus harrisii* .

Trait	Value/category	Reference
Size	Introduced areas: Max*: ♂ 22.8 mm, ♀ 20.2 mm	*This study
	Range: ♂ 1.8–22.9, ♀ 1.8–20.2 mm	Fowler et al. 2013, Turoboyski 1973
	Native areas: ♂ 4.1–14.6 mm, ♀ 4.4–12.6 mm	Ryan 1956
Size of maturity	Introduced areas: 8.4mm*, 4–5mm	*This study, Turoboyski 1973, Williams 1984 Ryan 1956
	Native areas: ♂ 4–5 mm, ♀ 4.4–5.5 mm	
Time to maturity	0.5 yr.	Williams 1984
Reproductive type	Sexual repr. (Gonochoristic)	Derived
Developmental type	Ovoviviparous	Derived
Larval type	Lecitotrophic (actively feeding)	Williams 1984
Larval duration	16 days (~ 30d in fully marine areas), 4 stages	Williams 1984
Larval migration	Vertical migration	Petersen 2006
Reproductive season	June – August (temp. dependent)	Fowler et al. 2013, *This study
Egg production	1200–4800 eggs (environmental-dependent)	Turoboyski 1973, *This study
*Trophic level	Primary consumers: ind. < 12mm Secondary consumers: ind.>12mm	*This study
*Stable isotope values	Average(sd) $\Delta^{13}C$: -18.4 ± 1.64 (ind.<12mm) -22.8 ± 1.4 (ind. >12mm)	*This study
	Average(sd) $\Delta^{15}N$: 11.4 ± 1.2 (ind. <12mm) -14.0 ± 0.8 (ind. >12mm)	*This study
*Diet (include ontogenetic shift)	Polychaetes (e.g. *Hediste* sp.) Crustaceans (e.g. *Gammarus* spp.) Molluscs (e.g. *Macoma balthica*) Detritus	*This study, Turoboyski 1973, Czerniejewski and Rybczyk 2008, Hegele-Drywa and Normant 2009
Resource capture method	Maxillipeds, maxillae, mandibles (adult), suspension feeder (larvae)	Derived, Williams 1984
Living habit	Epibenthic, Infauna	Derived
Mobility	Mobile	Derived
Movement type	Crawler, Burrower	Derived, *This study
Migration	Potentially to deeper waters in winter	Turoboyski 1973
Ecological information		
Salinity tolerance	0.5 – >20 psu	Boyle et al. 2010, Ryan 1956
	2.5 – 40 psu (larvae lab)	Costlow et al. 1966
Temperature tolerance	15 – 35 ºC (larvae lab)	Costlow et al. 1966
	at least +4 ºC (adult)	Derived from Finnish water temperatures in winter
Depth range	0–20m (max 37m)	Hegele-Drywa and Normant 2014,
Habitat preferences	Various: e.g. debris on seafloor, canopy-forming algae such as bladder-rack, mud, gravel, oyster and mussel reefs.	*This study, Fowler et al. 2013

lives in or on the top 1 cm of the sediment; and smaller crabs consume both detritus and plant material (Table 5). Furthermore, another trait that was found among the typical benthic species characteristics was diffusive mixing as a bioturbation mode (Törnroos and Bonsdorff 2012). While bioturbation by Harris mud crab at the sediment-water interface has not been investigated directly, the normal movements and feeding on the surface (Turoboyski 1973; Nurkse et al. 2015) most certainly moves sediments around (Kristensen et al. 2012). On the other hand, the burrowing behavior of *R. harrisii* (Turoboyski 1973; Peterson 2006; Fowler et al. 2013) may represent more elaborate bioturbation effect similar to regenerator or gallery-diffusers that aid bio-irrigation (Kristensen et al. 2012) such as fiddler crabs (Huang et al. 2007). *R. harrisii* matures in about half a year in the Baltic Sea (Turoboyski 1973) and has lecitotrophic larval development (Table 5), which are some of the less common characteristics of the northern Baltic Sea macrofauna (Valanko et al. 2010; Törnroos and Bonsdorff 2012), and may in part explain its success in its new environment.

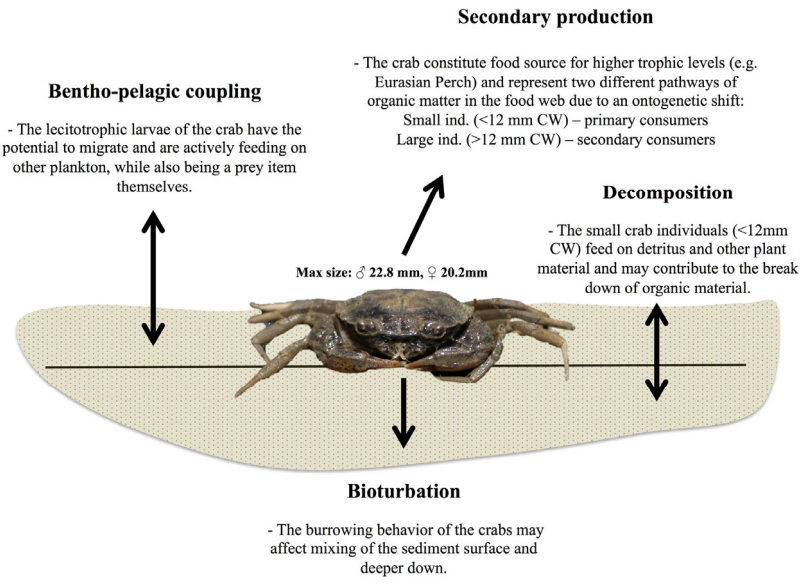

Figure 4. Conceptual figure showing ecosystem functions, to which the non-indigenous *Rhithropanopeus harrisii* potentially could contribute, based on its species-specific traits.

Sharing these traits with the natural macrofaunal community does not mean that the effect of *R. harrisii* on the functioning of the benthic ecosystem could not substantially differ from other benthic species (e.g. in terms of rates). However, it does suggest that the Harris mud crab qualitatively adds to the already present functional (trait) diversity, rather than bringing in something completely new. Disentangling this type of trait information further, in relation to ecosystem functions (Symstad et al. 2003; Violle et al. 2007; Reiss et al. 2009) will help broaden our understanding of the many roles of species in ecosystems (Hooper et al. 2005). Using the species-specific traits (Table 5), it is possible to conceptually illustrate the ecosystem functions of the non-indigenous *R. harrisii* (Figure 4). It is consumed by common predators, e.g., Eurasian perch (*Perca fluviatilis* Linnaeus, 1758), pikeperch (*Sander lucioperca* (Linnaeus, 1758)), and fourhourned sculpin (*Myoxocephalus quadricornis* (Linnaeus, 1758)) (Fowler et al. 2013), and thus contributes to secondary production. It has a role in bioturbation of the surface layer of the sediment. Due to its lecitotrophic larval mode, it would be involved in benthic-pelagic coupling as larvae both consume other zooplankton and are prey for both benthic and pelagic organisms (Marcus and Boero 1998; Raffaelli et al. 2003). Finally, the consumption of detritus and other plant material results in a breakdown and excretion of organic matter, which subsequently is available to the meiofaunal and bacterial community. Whether the net effect of *R. harrisii* on these ecosystem functions is positive and/or negative, remains to be investigated. Non-indigenous species can affect ecological processes positively and negatively (Thomsen et al. 2015). For example, modelling work (Norkko et al. 2012) suggests the introduced spionid polychaete *Marenzelleria* spp. may enhance phosphorus retention in sediments and thus reduce phosphorus release from bottom waters. This could be interpreted as positive driver of change influencing the function of the system (Norkko et al. 2012; Kauppi et al. 2015). Previously work on *R. harrisii* have stressed potential negative effects, such as the species possibility to displace native organisms (Zaitsev and Öztürk 2001; Fowler et al. 2013; Nurkse et al. 2015). As demonstrated in this study, *R. harrisii* may also contribute positively to the ecosystem functioning, especially in a species-poor system such as the Baltic Sea.

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